Number 312
March 16, 1979

CONTRIBUTIONS IN SCIENCE
NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

# *PROMYLAGAULUS*, PROGRESSIVE APLODONTOID RODENTS OF THE EARLY MIOCENE

*By* John M. Rensberger

Published by the NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY • 900 EXPOSITION BOULEVARD • LOS ANGELES, CALIFORNIA 90007

CONTENTS

Abstract ..... 3
Abbreviations of Institutions ..... 3
Dental Nomenclature ..... 3
Methods ..... 4
Morphologic Relationships ..... 4
Systematic Paleontology: Order RODENTIA,
Superfamily Aplodontoidea Matthew 1910, Family Mylagaulidae Cope 1881
*Promylagaulus* McGrew 1941 ..... 13
*Promylagaulus riggsi* McGrew 1941 ..... 14
*Promylagaulus lemhiensis* Nichols 1976 ..... 14
*Promylagaulus ovatus* new species ..... 15
*Promylagaulus montanensis* new species ..... 15
*Promylagaulus* sp. ..... 16
Phyletic Relationships of the Species ..... 16
Acknowledgments ..... 17
Literature Cited ..... 17

The *Science Bulletin* and *Contributions in Science* of the Natural History Museum of Los Angeles County were merged into a single imperial octavo serial, retaining the name *Contributions in Science* and beginning with Number 301.

This serial has been newly formatted for maximum use of typography and illustrations per page, and sized for maximum use of paper. All photography has been produced utilizing a 200-line screen for detail.

Since most institutions rebind *Contributions in Science* collectively into hardbound volumes, and many researchers using them desire to photocopy material, two new features have been incorporated into the new format. A suggested citation line provides the abbreviated serial title, year, number of publication, and total pagination, and appears in the lower left corner of each page; and pages of *Contributions in Science* have been printed off-center to provide a two-inch gutter between adjacent pages for easier accessibility in photocopying.

ISSN: 0459–8113

Suggested Citation: *Contrib. Sci. Natur. Hist. Mus. Los Angeles County*. 1979. **312**:1–18.

*Contributions in Science* are articles in the earth and life sciences, presenting results of original research in Natural History. *Science Bulletin* (Numbers 1–30; 28 June 1965 to 10 April 1978) and *Contributions in Science* (Numbers 1–300; 23 January 1957 to 16 June 1978) were merged into a single imperial octavo serial beginning with Number 301.

# *PROMYLAGAULUS*, PROGRESSIVE APLODONTOID RODENTS OF THE EARLY MIOCENE[1]

*By* John M. Rensberger[2]

ABSTRACT: *Promylagaulus*, until recently represented by only a single described species of uncertain age, *P. riggsi*, is a diverse and rather widely distributed genus, most members of which seem to occur in a restricted interval of the early Miocene. Of the two new species described here, *P. ovatus* is from an upper part of the Monroe Creek Formation in South Dakota, and *P. montanensis* occurs in a restricted interval in the Deep River Formation of Montana. A form from northern Wyoming, when better known, may represent another species. Each of these three occurrences is within the *Entoptychus-Gregormymys* Concurrent-range Zone of Fisher and Rensberger (1972). *P. lemhiensis*, from northern Idaho, is apparently from an only slightly older interval.

These species differ in hypsodonty, size and lophodonty. No trend toward characteristics definitive of the Mylagaulidae is evident among these species and a number of features indicate that *Promylagaulus* was not ancestral to the later mylagaulids. Although similar in a number of characteristics to an earlier and more primitive aplodontoid, *Meniscomys*, *Promylagaulus* frequently retained at least one primitive feature that was absent in the earliest known members of *Meniscomys*.

A few years ago, a biostratigraphic study of the Deep River and Fort Logan formations of Montana was undertaken in order to more clearly correlate Oligo-Miocene sequences of vertebrates of the far west with faunas within and east of the Rocky Mountain region. One of the taxa recovered in the course of this study is an aplodontoid rodent resembling specimens referred to *Promylagaulus riggsi* McGrew, described from the Monroe Creek Formation of South Dakota by J.R. Macdonald (1963, 1970) and L. Macdonald (1972), and *P. lemhiensis* Nichols (1976) from the early Miocene of Idaho.

The problem of assessing the relationships of small samples of *Promylagaulus* is difficult because the cheek teeth in this genus are high crowned and complex, with numerous enamel bordered lakes of different depths and which vary in size and shape with wear. The dentition in the type specimen of *P. riggsi* (McGrew 1941) has few characteristic features that are not made ambiguous by the advanced stage of wear. The more recently described specimens of *Promylagaulus* were reported upon in papers devoted to entire faunas and the comparative morphologies have not as yet been presented in detail. This paper compares the new material of *Promylagaulus* from the Deep River Formation with that from South Dakota and Idaho, and presents additional evidence concerning the relationship of these forms.

## Abbreviations of Institutions

| | |
|---|---|
| AMNH | American Museum of Natural History |
| FMNH | Field Museum of Natural History |
| ISU | The Museum, Idaho State University |
| LACM | Los Angeles County Museum of Natural History |
| SDSM | South Dakota School of Mines and Technology |
| UM | Department of Geology, University of Montana |
| UWBM | University of Washington, Burke Memorial Washington State Museum |

## Dental Nomenclature

The principal cusps of the cheek teeth in *Promylagaulus* (Fig. 1) correspond to those of *Haplomys* (Rensberger 1975: Fig. 1). Whereas the major cusps are homologous to those of other groups of rodents, the enamel inflections, fossettes and fossettids are frequently not homologous. Different authors have applied the terminology used by Stirton (1935) for the castorids to the mylagaulids, but in conflicting ways. Because of fundamental differences in the origins of the inflections and lakes in the castorids and aplodontoids, there is no obvious and natural way to transfer a number of the names from the former to the latter. Rather than introduce new terms for these structures in the aplodontoids at this time, and to avoid confusion with the several usages of the castorid nomenclature, I have simply used descriptive terms based upon the position of the structure with reference to the center of the tooth (Fig. 1). Thus the structures in any of the four quadrants are prefixed by anterolingual, posterolingual, etc., and those falling in the midsection of a side by labial, lingual, anterior or posterior. An advantage of this method is that when applied to fossettes and fossettids, it lends itself to situations in which a structure originates in different ways. For example, within a single species of *Promylagaulus* there may be both anterolingual and posterolingual fossettids on $P_4$, or there may be only a lingual fossettid in those positions, depending upon whether or not the mesostylid is joined to the mesoconid by a crest. This

[1]Review Committee for this Contribution:
Craig Black
Mary Dawson
David Whistler

[2]Burke Memorial Washington State Museum and Department of Geological Sciences, University of Washington, Seattle 98195.

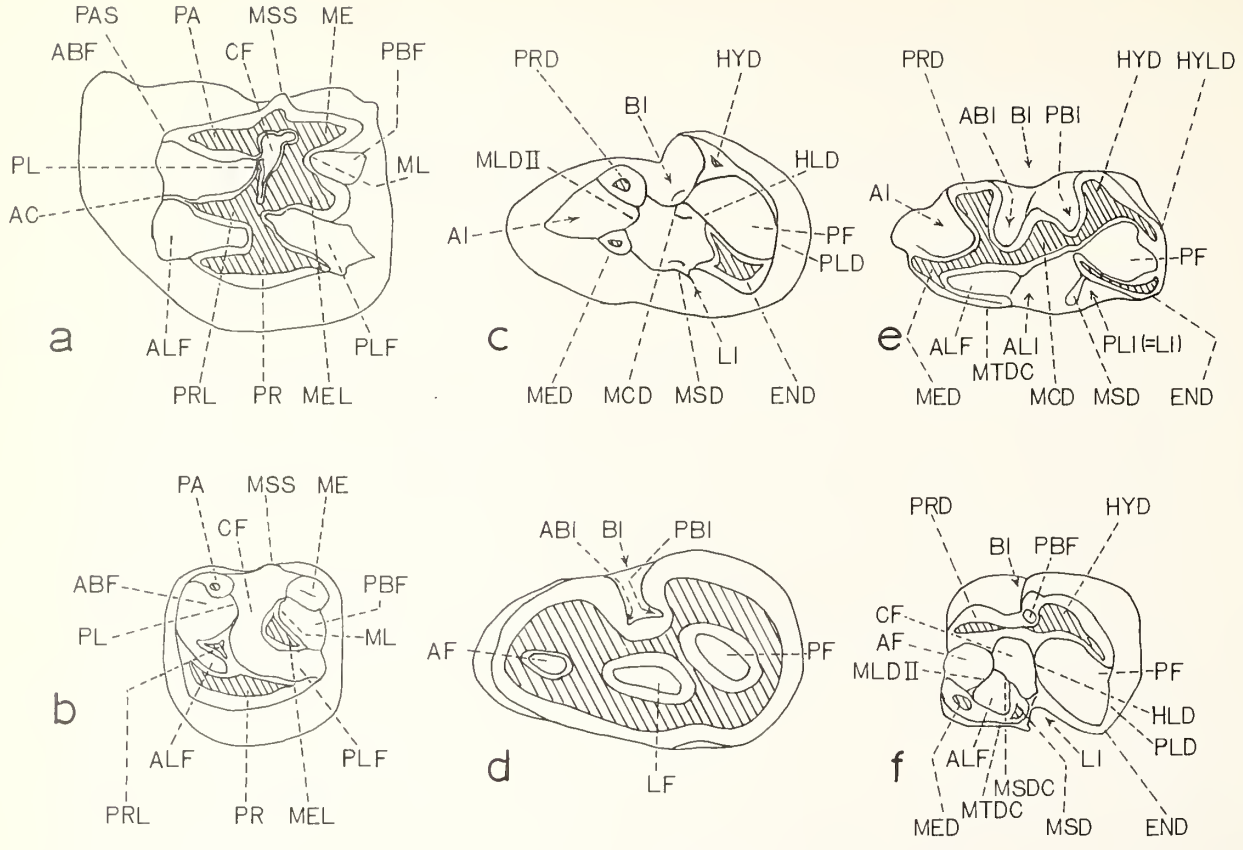


FIGURE 1. Nomenclature of occlusal structures in *Promylagaulus*. *a*–left $P^4$; *b*–left $M^1$ or $M^2$; *c*–little worn right $P_4$; *d*–well worn right $P_4$; *e*–right $DP_4$; *f*–right $M_1$ or $M_2$. Cross hatching = dentine; labial side toward top, anterior toward left. ABF = anterolabial fossette (-id); ABI = anterolabial inflection; AC = anterocone; AF = anterior fossettid; AI = anterior inflection; ALF = anterolingual fossette (-id); ALI = anterolingual inflection; BI = labial inflection; CF = central fossette (-id); END = entoconid; HLD = hypolophid; HYLD = hypoconulid; HYD = hypoconid; LF = lingual fossettid; LI = lingual inflection; MCD = mesoconid; ME = metacone; MED = metaconid; MEL = metaconule; ML = metaloph; MLDII = metalophulid II; MSD = mesostylid; MSDC = mesostylid crest; MSS = mesostyle; MTDC = metastylid crest; PA = paracone; PAS = parastyle; PBF = posterolabial fossette; PBI = posterolabial inflection; PF = posterior fossettid; PL = protoloph; PLD = posterolophid; PLF = posterolingual fossette; PLI = posterolingual inflection; PR = protocone; PRD = protoconid; PRL = protoconule (paraconule).

method somewhat simplifies the terminology in a group in which the occlusal structure can be very complex.

## METHODS

The most objective information bearing on the relationship of the fossil jaws, teeth and skull representing *Promylagaulus* is the stratigraphic-geographic occurrence of the elements. Specimens from a single geographic and stratigraphic position and among which there is no evidence of a significant discontinuity in morphology were probably members of a single population or very closely related ones. This information, together with the complex combinations of morphologic similarities and dissimilarities presented in the following sections show that at least four distinct taxonomic groups are represented.

The distinct geographic-stratigraphic associations are:

Deep River Fm., central Montana, *(P. montanensis)*
Lemhi Valley, western Montana, *(P. lemhiensis)*
Anthills locality, uppermost Monroe Creek Fm., S. Dakota, *(P. ovatus)*
Specimen SDSM 6277, Monroe Creek Fm., S. Dakota, *(P. ovatus)*
*P. riggsi*, unknown locality, S. Dakota

## MORPHOLOGIC RELATIONSHIPS

The material from the Deep River Formation consists of two right mandibles: UWBM 38075, with $P_4$–$M_3$; and UWBM 38103, with a lower incisor fragment and $DP_4$–$M_2$. The specimens are from approximately the same stratigraphic position in a 5 to 7 m thick massive sandstone at a single exposure. Although the relatively little worn and moderately worn occlusal patterns of the molars in the two specimens differ greatly, analogous differences are also present among the isolated teeth reported from an anthill locality in the Monroe Creek Formation of South Dakota and referred to *Promylagaulus riggsi* by L. Macdonald (1972). The specimens from the Deep River Formation probably represent a single population, or at least closely related ones.

### LOWER INCISOR

The enamel face of the incisor in the Deep River taxon is broad and only slightly convex transversely. It closely resembles that of *Meniscomys hippodus* Cope, of the John Day Formation, except that the width is somewhat greater, consistent with the overall larger size of the mandible. The incisor is wider and slightly flatter than that of SDSM 6277, cf. *Promylagaulus riggsi*

(Macdonald 1970:33) from South Dakota, a specimen of smaller overall size.

## Deciduous Lower Premolar

The $DP_4$ of the Deep River form (UWBM 38103) is well worn but still retains several fossettids (Fig. 2a). A central anterior fossettid is triangular with one angle in a posterior position and the remaining angles in anterolabial and anterolingual positions. The anterolingual corner of the fossettid is not quite closed at the existing stage of wear. The anterior fossettid in SDSM 6277 also opens anterolingually, although the fossettid is more worn and less triangular than in the specimen from Montana. In a specimen of *Meniscomys hippodus* (UWBM 29160), the anterior fossettid is oval, narrower transversely than that in SDSM 6277 or the Deep River form, and opens directly craniad. Three unworn to lightly worn deciduous lower premolars, 117384, 117436 from the anthill locality (LACM 1871 = SDSM 6229) were not described by L. Macdonald (1972), although they are questionably assigned on the specimen record to *Promylagaulus riggsi*. Although pronounced morphologic differences exist among these specimens, they probably belong to the taxon represented at that loeality by permanent teeth, as will be shown below. The anterior fossettid or inflection in the specimens of $DP_4$ from the anthill collections (Fig. 3b) is triangular, as in the Deep River form,

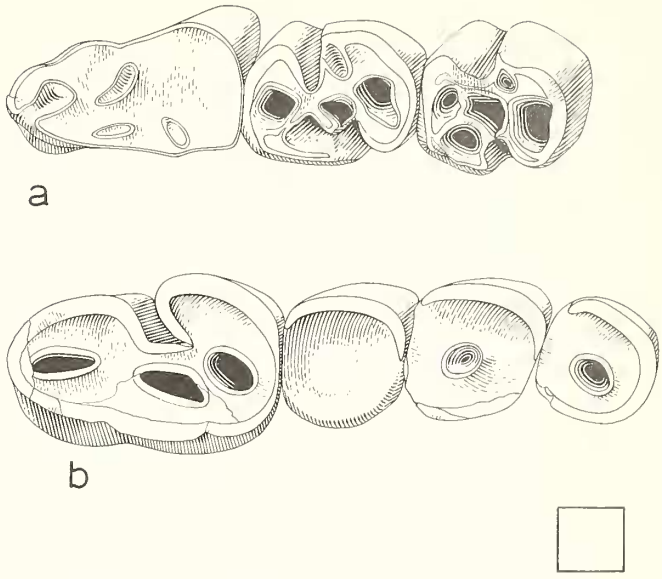


FIGURE 2. *Promylagaulus montanensis*. *a*–occlusal view right $DP_4$–$M_2$, UWBM 38103; *b*–occlusal view right $P_4$–$M_3$, UWBM 38075. Both specimens from level 1 of locality Spring Creek 1 (UWBM A5867), Deep River Formation, Montana. Labial side toward top of figure. Scale = 1 mm. Drawing by Mark Orsen.

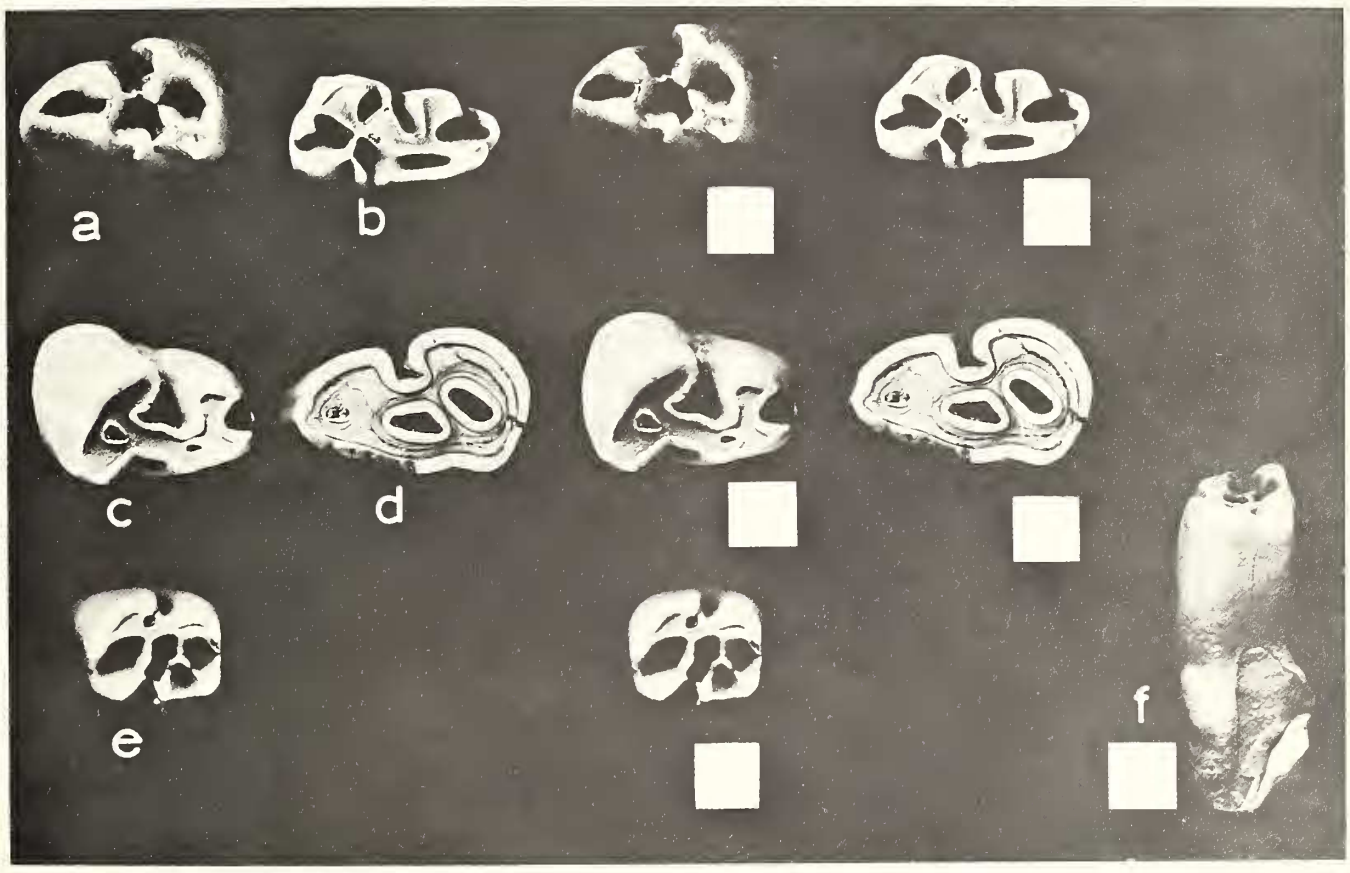


FIGURE 3. *Promylagaulus ovatus*, lower cheek teeth. *a*–occlusal view little worn right $P_4$, LACM 117372; *b*–occlusal view left $DP_4$, LACM 117436; *c*–occlusal view worn left $P_4$, LACM 117368; *d*–occlusal view worn right $P_4$, LACM 117370; *e*–occlusal view left $M_1$, LACM 117435; *f*–same, posterior view. All except *f* stereo pairs. Labial side toward top of figure. Scale = 1 mm.

TABLE 1

Length, Width of $P_4$; Depth of Labial Enamel on $P_4$ (mm)

| MUSEUM NUMBER | LOCALITY | LP | WTR | WTA | DLEP | DLEP/LP |
|---|---|---|---|---|---|---|
| UWBM 38075 | Deep River Fm (UWA 5867) | 4.1 | 2.2 | 2.7 | 2.8 | 0.68 |
| ISU 18594 | Lemhi Valley (ISU 59003) | 4.7 | 1.9 | 2.7 | 2.0 | 0.43 |
| ISU 18601 | Lemhi Valley (ISU 59003) | 5.0 | 2.2 | 3.0 | 2.2 | 0.44 |
| AMNH 56333 | Darton's Bluff* | 3.6 | 1.8 | 2.2 | — | — |
| LACM 9340 | Wolff Ranch (LACM 20051) | 3.8 | 2.0 | 2.4 | — | — |
| LACM 9342 | Wolff Ranch (LACM 20051) | 3.5 | 1.8 | 2.2 | 1.9 | 0.54 |
| LACM 23530 | Anthill (LACM 1871) | 3.4 | 1.5 | 1.9 | — | — |
| LACM 117367 | Anthill (LACM 1871) | 3.7 | 1.9 | 2.0 | 1.8 | 0.49 |
| LACM 23532 | Anthill (LACM 1871) | 3.5 | 1.7 | 1.9 | 1.8 | 0.51 |
| LACM 117437 | Anthill (LACM 1871) | 3.5 | 1.6 | 2.2 | 1.8 | 0.51 |

LP = anteroposterior length near base of crown.
WTR = transverse width of trigonid measured perpendicular to vertical axis of tooth.
WTA = transverse width of talonid, measured perpendicular to vertical axis of tooth.
DLEP = depth of labial enamel measured ventrad from apex of posterior dentinal tract.
* = measurements taken from published illustration (McKenna and Love 1972).

although the sequence of closure of the two anterior corners is variable.

An arcuate anterolabial inflection in UWBM 38103 lies in a transverse orientation near the anteroposterior center of $DP_4$ and anterior to the mesoconid. Opposite the inflection and near the lingual margin of the tooth is an anteroposteriorly aligned fossettid that is represented in *Meniscomys hippodus* by a shallow valley which doesn't form a fossettid. In both UWBM 38103 and *M. hippodus* the fossettid or valley is bounded lingually by an elongate metastylid crest at the margin of the tooth. Both the arcuate anterolabial fossettid and the elongate anterolingual fossettid are present in the teeth of the anthill locality (Fig. 3b). However, in one specimen of the latter the mesoconid lacks the labial spur that isolates the anterolabial fossettid in the other specimens.

The base of the posterolingual inflection is barely preserved in the specimen from the Deep River Formation. It lies near the lingual margin of the tooth between the areas of the entoconid and the mesostylid. The margin of the tooth is extended as a small, lingual protuberance slightly anterior to the opening of the inflection. These structures are similar to conditions present in the specimens of both *Meniscomys hippodus* and the anthill collection. The teeth in the anthill collection still retain the posterolingual fossettid, which is more posteriorly situated with respect to the posterolabial fossettid than is that in *M. hippodus*. The hypoconid of the specimens in the anthill collection is more anteriorly situated and less expansive posterolabially than in *M. hippodus* (Fig. 3b). It is this feature which relates the deciduous premolars most clearly to the molars in the anthill collection.

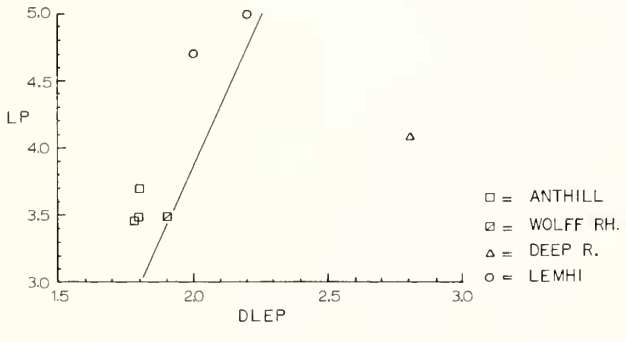


FIGURE 4. Bivariate plot of depth of labial enamel below highest point of posterior dentinal tract (DLEP) and anteroposterior length (LP) of $P_4$ in specimens of *Promylagaulus* from Anthill (LACM 1871), Wolff Ranch (LACM 2005), Deep River (Spring Creek 1, level 1; UWBM A5867) and Lemhi Valley (UM V-7303 = ISU 59003) localities.

## Lower Premolar

The worn permanent premolar from the Deep River Formation is larger than those from the anthill collection, but its size, especially length, is exceeded by those from Lemhi Valley (Table 1). The anterior fossettid in the worn $P_4$ of UWBM 38075 from the Deep River Formation (Fig. 2b) is anteroposteriorly elongate and narrow, but slightly expanded anteriorly. In the Lemhi collection the fossettid is also elongate, but in SDSM 6277 and the numerous isolated teeth of the anthill collection (Fig. 3c,d) the fossettid is wider and shorter than that in the Deep River form.

The labial inflection in UWBM 38075 is directed posterolinguad, toward the center of the tooth (Fig. 2b). It ends internally at the flat surface of the mesoconid and lacks an anterior branch, but a narrow posterior portion representing the inflection posterior to the mesoconid in *Haplomys* (Rensberger 1975:6), the posterolabial inflection, extends to within 0.1 mm of the posterior fossettid. The hypoconid is posterolabially compressed and anteriorly expanded so as to contribute to the posterolingual trend of the labial inflection. In the Lemhi collection, SDSM 6277 and the unworn and little worn teeth in the anthill collection (Fig. 3a–d), the hypocone is similarly compressed and anteriorly expanded, the labial inflection abuts a normally flat mesoconid with little if any tendency to extend anteriad, and a narrow branch of the labial inflection extends behind the mesoconid toward the posterior fossettid, as in the Deep River form. There

TABLE 2

Ratios of Size of Posterior and Lingual Fossettids to Width of $P^4$

| MUSEUM NUMBER | LOCALITY | WP | WPF4 | WPF4/WP | WLIF4 | WLIF4/WP | WC | WC/WP |
|---|---|---|---|---|---|---|---|---|
| ISU 18601 | Lemhi Valley (ISU 59003) | 2.7 | 1.1 | 0.41 | 0.8 | 0.30 | 1.8 | 0.67 |
| LACM 117370 | Anthill collection (LACM 1871) | 2.2 | 0.7 | 0.32 | 0.6 | 0.27 | 1.5 | 0.68 |
| LACM 117352 | Anthill collection (LACM 1871) | 2.2 | 0.8 | 0.36 | 0.6 | 0.27 | 1.4 | 0.64 |
| LACM 117366 | Anthill collection (LACM 1871) | 2.2 | 0.7 | 0.32 | 0.6 | 0.27 | 1.3 | 0.59 |
| UWBM 38075 | Deep River Fm (UWA 5867) | 2.7 | 0.8 | 0.30 | 0.6 | 0.22 | 1.5 | 0.55 |

WP = transverse width of $P_4$ across talonid.
WPF4 = transverse width of posterior fossettid on $P_4$, measured from outer margin of enamel.
WLIF4 = transverse width of lingual fossettid on $P_4$, measured from outer margin of enamel.
WC = transverse width of $P_4$ in center, from posterior end of posterolabial inflection.

is usually no mesoconid process on the hypoconid of *P. lemhiensis* or most of the specimens from the Monroe Creek Formation; however in several specimens from the anthill site a crest from the mesoconid joins the latter to the anterior process of the hypoconid to form a small posterolabial fossettid.

In *Meniscomys hippodus,* in contrast to many of the specimens from Montana, Idaho and South Dakota, the labial process of the mesoconid is persistent and joins at depth with a process from the hypoconid to enclose the posterolabial inflection as a fossettid. This tendency is present in the stratigraphically lowest of the known specimens of *Meniscomys*. As a consequence of this condition, the labial inflection in worn teeth of *M. hippodus* is confined to a transversely aligned slot that internally represents only the anterolabial inflection.

The posterior fossettid is still present in the moderately advanced stage of wear of UWBM 38075 (Fig. 2b). The lake is oval, with the long axis trending anterolabiad. The posterior fossettid in the teeth in the anthill collection is larger, relative to the width of the tooth (Table 2), than in the Deep River form (Fig. 3d). The fossettid is largest relative to tooth width in the Lemhi collection. In SDSM 6277 and *P. lemhiensis,* the fossettid is bounded in an early stage of wear by a distinct cusp joining the entoconid and mesoconid and forming the hypolophid, but in the anthill collection this cusp is much reduced.

A posteriorly elongate but slightly triangular lingual fossettid is present in the $P_4$ of the UWBM 38075. This fossettid is transversely wider relative to tooth width and more oval in the Lemhi and anthill collections (Table 2). The lake is bounded lingually by the surface of the metastylid crest, anterolabially by the surface of the mesoconid and posterolabially by the hypolophid (Fig. 2b). In all forms the posterolingual inflection extends as a shallow groove well below the stage of wear at which the fossettid closes. A considerable amount of variation in the structures bounding the fossettid is present among the little worn anthill specimens and SDSM 6277. Usually a strong metastylid crest (Fig. 3a) extends caudad to join either the hypolophid or a mesostylid cusp (or crest). There may be no mesostylid. When a mesostylid is present, it may be joined to both the metastylid crest and the mesoconid, so that the fossettid is restricted to an anterolingual position, at least in the upper part of the crown. In individuals in which the metastylid crest is undeveloped (Fig. 3c), the mesostylid tends to be flanked by anterolingual and posterolingual inflections which may not form fossettids at all, or only a small one. Specimens in the anthill collection in which the metastylid crest dominates and connects to the hypolophid (Fig. 3a, d) resemble those of the Lemhi collection and probably exhibit the structure that would be shown by UWBM 38075 in an earlier stage of wear.

In the primitive species of *Meniscomys* from the John Day Formation (Rensberger, in manuscript) individuals both with and without a metastylid crest are present. Those with the metastylid crest may lack a mesostylid, or if the latter is present, have an incipient lingual fossettid communicating (in the absence of a union between mesostylid and mesoconid) with the posterolingual fossettid. Individuals of later populations in the John Day Formation consistently have a mesostylid bounded by anterolingual and posterolingual inflections which do not close with wear to form fossettids.

The hypsodonty of the premolar in the Deep River form, as indicated by the depth of the labial enamel plate beneath the top of the posterior dentinal tract, exceeds that in the other collections (Fig. 4 and Table 1). Although the absolute length of the plate in the Lemhi collection slightly exceeds measurements in the anthill collection, the Lemhi specimens are the more brachyodont, as is shown by Figure 4 and the ratio of enamel length to tooth length (DLEP/LP in Table 1).

A locality (LACM 2005) northeast of Wolff Ranch in the Wounded Knee region of South Dakota yielded three lower cheek teeth, two of which are premolars which are not distinguishable in occlusal pattern or hypsodonty (Table 1) from the teeth in the anthill collection. The museum records indicate the specimens were derived from the Sharps Formation, but the color of the enamel is dark brown, like that of most of the teeth from the anthill collection in the Monroe Creek Formation.

A pair of mandibular rami with heavily worn teeth having a pattern similar to that of UWBM 38075 were found at Darton's Bluff, Big Horn Mountains, northern central Wyoming (McKenna and Love 1972:23). The wear is such that only two enamel lakes, the anterior and lingual fossettids, remain on the $P_4$ (McKenna and Love 1972: Figs. 15, 16), which makes difficult determination of the relationships of the form. The anteroposterior and transverse dimensions are smaller than those of UWBM 38075 and the Lemhi specimens but compare favorably with those from the anthill collection (Table 1).

TABLE 3

Length and Width of $M_1$, $M_2$, $M_3$ (mm)

| MUSEUM NUMBER | LOCALITY | uL1 | uL2 | uL3 | uW1 | uW2 | uW3 | wL1 | wL2 | wL3 |
|---|---|---|---|---|---|---|---|---|---|---|
| ISU 18594 | Lemhi Valley (ISU 59003) | 2.8 | 2.6 | 2.0 | 2.1 | 2.1 | 1.6 | — | — | — |
| UM 5193 | Lemhi Valley (UMV 7303) | — | — | — | — | — | — | — | 2.4 | 1.9 |
| UWBM 38103 | Deep River Fm. (UWA 5867) | 2.7 | 2.3 | — | 2.0 | 2.0 | — | — | — | — |
| UWBM 38075 | Deep River Fm. (UWA 5867) | — | — | — | — | — | — | 1.9 | 2.2 | 1.8 |
| AMNH 56333 | Darton's Bluff (AMNH) left teeth† | — | — | — | — | — | — | 2.0 | 2.3 | 1.7 |
| SDSM 6277 | Monroe Creek Fm. (SDSM V-6210) | 2.4 | 2.2 | — | 1.8 | 1.7 | — | — | — | — |
| LACM 23534 | Anthill (LACM 1871) | 2.8* | — | — | 2.1 | — | — | 2.3 | — | — |
| LACM 117441 | Anthill (LACM 1871) | 2.4 | — | — | 1.9 | — | — | 1.7 | — | — |
| LACM 117435 | Anthill (LACM 1871) | — | 2.2 | — | 1.8 | 1.7 | — | — | — | — |
| LACM 117374 | Anthill (LACM 1871) | — | 2.4 | — | — | 2.1 | — | — | 2.3 | — |
| LACM 117373 | Anthill (LACM 1871) | — | 2.2 | — | — | 1.9 | — | — | 2.2 | — |
| LACM 117415 | Anthill (LACM 1871) | — | — | — | — | — | — | — | — | 1.8 |
| LACM 117404 | Anthill (LACM 1871) | — | — | — | — | — | — | — | — | 1.7 |
| LACM 117406 | Anthill (LACM 1871) | — | — | — | — | — | — | — | — | 1 6 |
| UCMP 75554 | *Meniscomys hippodus* (UCMP V-6351) | 2.0 | 2.0 | 1.9 | 1.8 | 1.8 | 1.5 | — | — | — |
| UCMP 105101 | *Meniscomys hippodus* (UCMP V-66104) | — | — | — | — | — | — | 1.7 | 2.0 | 2.1 |
| UCMP 105104 | *Meniscomys hippodus* (UCMP V-66104) | — | — | — | — | — | — | 1.8 | 2.1 | 2.1 |

u = unworn or only moderately worn occlusal dimension.
w = well worn or dimension taken near base of crown.
L = anteroposterior length.
W = transverse width.
1, 2, 3, = $M_1$, $M_2$, $M_3$.

* by far the largest molar in the anthill collection.
† measurements taken from published illustration.

## Lower First and Second Molars

The lower molars of the Deep River form are larger than those of the anthill collection but slightly smaller than those of the Lemhi collection (Table 3). In $M_{1-2}$ of UWBM 38103 (Fig. 2a), an anterior fossettid is bounded posterolingually by the metalophulid II, which extends to the apex of the metaconid. The anterior fossettid in SDSM 6277 and the anthill and Lemhi collections is similarly formed.

In *Meniscomys* from the John Day Formation, only the labial arm of the metalophulid II is present. A slight expansion in the metalophulid II is present at the center of the tooth in the primitive species but no crest extends to the metaconid. In some individuals the expansion is stronger and restricts the anterior fossettid, but in others the fossettid is unrestricted. Occasionally the metaconid in *M. hippodus* is expanded and contacts the metalophulid II to create a small anterior fossettid in late stages of wear. In *M. hippodus,* the metalophulid II is continuous with a crest from the mesostylid; in UWBM 38103, the Lemhi collection, the anthill collection and SDSM 6277 the mesostylid crest appears to be an accessory to the metalophulid II, for it joins the latter at an angle.

The metastylid crest is stoutly developed in the Deep River form (Fig. 2a). It is slightly expanded opposite the middle of the tooth, in the position occupied by the mesostylid in primitive aplodontoids. In $M_1$ the crest extends 0.4 mm posterior to a transverse line through the center of the mesostylid expansion, thereby partially closing the lingual inflection. The metastylid crest of SDSM 6277 and the anthill collection (Fig. 3e) is similar but more lightly developed and seldom extends beyond the mesostylid. Though worn, the crest in ISU 18594 appears to have been less prominent than that in the Deep River form. The metastylid crest is absent in *Meniscomys hippodus*. However, in more primitive individuals of *Meniscomys* from the John Day Formation, the metastylid crest may be present as a very rudimentary structure.

An anterolingual fossettid is present in the Deep River form, the Lemhi collection and SDSM 6277, and is variably present in the anthill collection. It is bounded by the metalophulid II, the diagonally directed mesostylid crest, and the metastylid crest. When the anterolingual fossettid is not complete in the anthill collection, this is usually the result of weak development of the mesostylid crest. In $M_1$ of the Deep River specimen, the mesostylid crest from the metalophulid II is stout but barely makes occlusal contact with the mesostylid. In *M. hippodus* an anterolingual fossettid is seldom formed because the metalophulid II does not extend toward the metaconid.

In the specimen from the Deep River Formation, the Lemhi collection, SDSM 6277, the anthill collection, and *Meniscomys hippodus,* the central fossettid is the deepest of the four or five fossettids. In the $M_1$ of a primitive form of *Meniscomys* from the John Day Formation, a lingual inflection is present but there is

little or no indication of a crest tending to enclose a central fossettid. In more advanced forms a central fossettid is formed in $M_1$. In the $M_2$ of *Meniscomys* the central fossettid is usually closed.

The lingual inflection in $M_1$ and $M_2$ of the Deep River form is closed at the lingual extremity by a low crest forming a basin or shelf at the base of the inflection, well below the closure of the central fossettid (Fig. 2a). A small, shallow fossettid is formed at the base of this inflection on $M_1$, but is not quite formed on $M_2$. In SDSM 6277, ISU 18594 and most of the anthill collection, the shelf is absent and the inflection usually fades out at depth. A shelf may or may not be present in *Meniscomys hippodus;* in primitive specimens of *Meniscomys* from the John Day Formation a shelf tends to be present but does not enclose a fossettid.

The mesoconid in the Deep River specimen is a triangular cusp, with a heavy labial spur that joins the anterior margin of the hypoconid to enclose a very small, shallow posterolabial fossettid (Fig. 2a). The configurations in SDSM 6277 and the anthill collection are similar except that the mesoconid in $M_1$ is smaller and less distinct (Fig. 3e). The mesoconid spur is directed anterolabiad in the Deep River specimen, whereas it runs posterolabiad in SDSM 6277 and strongly so in the anthill specimens (Fig. 3e). In *Meniscomys hippodus* the mesoconid is a distinct cusp, but the structure connecting it with the hypoconid is a thinner crest than that in *Promylagaulus*.

The hypoconid in the Deep River form, the Lemhi collection, SDSM 6277, and the anthill collection is posterolabially compressed and, as in $P_4$, expanded anteriorly (Figs. 2a, 3e). In the Deep River specimen the anteroposterior expanse of the labial inflection is less than in the other specimens and more deeply incised medially, especially in $M_1$. The posterolophid is posteriorly expanded and convex in the specimens from Montana, Idaho and South Dakota, but the convexity is most pronounced, especially at the transverse midpoint of the crest, in the Deep River form. The hypoconid of *Meniscomys hippodus* is expanded rather than compressed posterolabially, and the posterior surface of the posterolophid is relatively straight.

The posterior fossettid in the specimen from Montana is polygonal in shape, owing to prominence of the hypoconulid and entoconid, with the long diameter aligned anterolabially. In SDSM 6277 and the anthill collection, the fossettid has the same orientation but is more smoothly oval in outline. In *Meniscomys hippodus* the posterior fossettid is more compressed than in any of the other forms and the long axis is aligned anteroposteriorly.

$M_1$ in the lightly worn dentition from the Deep River Formation, UWBM 38103, as in the intermediately worn specimen from the Lemhi Valley (ISU 18594), appears somewhat larger than $M_2$ (Fig. 2a). In the heavily worn dentition from Montana, UWBM 28075, $M_1$ is slightly smaller in occlusal dimensions than $M_2$ (Fig. 2b). $M_1$ in the little worn dentition of SDSM 6277 is slightly larger at the occlusal surface than $M_2$. The isolated lower molars of the anthill collection vary greatly in size, probably in part due to such positional variation. In little worn dentitions of *Meniscomys* from Oregon, $M_1$ and $M_2$ are almost equal in size. However, in well worn dentitions $M_1$ becomes relatively smaller, especially in anteroposterior length, than in UWBM 38075.

At the late stage of wear represented in the Deep River form (Fig. 2b), the labial inflection has disappeared and the occlusal edge of the labial enamel forms a thick crest extending from the anterolabial corner of $M_1$ or $M_2$ across the labial face and onto the posterior face. The remaining three-fifths or more of the occlusal margin in $M_1$ lacks enamel. An isolated bit of lingual enamel persists in $M_2$. The only fossettid remaining in these teeth is the central one in $M_2$. The molars at this stage are reduced in size and rather oval in shape.

In the teeth from the anthill collection, the basal enamel of the hypoconid region extends more prominently posterolabiad than in UWBM 38075, giving the teeth an angular outline that persists with wear. Furthermore, the posterior surface at depth is invaginated, marking a division between the vestigial roots which is not indicated in UWBM 38075 nor ISU 18594. In *Meniscomys hippodus,* the labial inflection persists into late stages of wear, and the teeth retain an angular outline.

Full measurement of the degree of hypsodonty in the molars from the Deep River Formation is impossible because the enamel is either partially hidden by alveolar bone, or much of it has been worn away. Judging from the amount of enamel remaining on $M_2$ of UWBM 38075, the ratio of enamel length to tooth width was greater than that in a specimen of the Lemhi collection (Fig. 5 and Table 4). The relative length of enamel is greater in the anthill collection than in the Lemhi collection. An isolated molar from another locality (SDSM V59) is less hypsodont than that of the Lemhi collection or those of the anthill collection and may be more closely related to *P. riggsi*. The depth of the labial enamel in *Meniscomys hippodus* is one-third or less that in the Lemhi or anthill collections. Although the type of *Promylagaulus riggsi* lacks the lower dentition, an indication of the degree of hypsodonty of this specimen relative to that of the other collections is obtainable from the upper dentition, described in a later section.

A thin layer of cement extends over the lower part of the enamel in several of the lower molars of the anthill collection, and a rather heavy layer extends at least 1.3 mm above the base of the lingual enamel on UM 5193 of the Lemhi collection. Cement extends perhaps 0.5 mm up the lingual enamel of $M_2$ in UWBM 38075.

The first and second molars of AMNH 56333, from Darton's Bluff, lack fossettids, owing to the advanced stage of wear. These teeth are oval in occlusal outline — slightly more so than in the less worn molars of UWBM 38075, and differ in this respect from the angular pattern in the anthill collection. In contrast to UWBM 38075, the lingual and posterior enamel in this specimen still persists in spite of the deeper stage of wear with

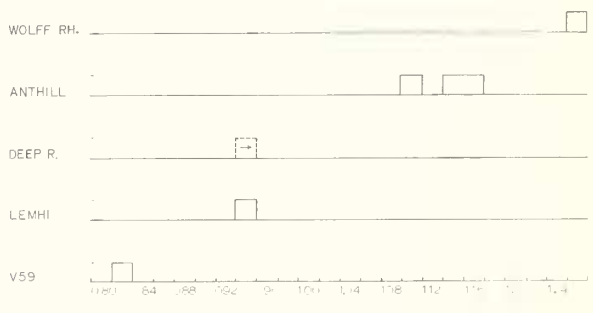


FIGURE 5. Frequency distributions of values of ratio of depth of labial enamel below highest point of posterior dentinal tract to transverse width of $M_1$ or $M_2$ in Promylagaulus. Localities are those in Fig. 4, plus SDSM V59. Base measurements for classes are listed. Arrow indicates incomplete measurement.

TABLE 4

Depth[1] of Labial Enamel on $M_1$, $M_2$ (mm)

| MUSEUM NUMBER | LOCALITY, TAXON | DE1 | DE2 | DE1/W1 | DE2/W2 |
|---|---|---|---|---|---|
| UWBM 38075 | Deep River Fm. (UWA 5867) | — | 2.0+ | — | >0.95 |
| ISU 18594 | Lemhi Valley (ISU 59003) | — | 2.0 | — | 0.95 |
| LACM 117435 | Anthill Collection (LACM 1871) | — | 2.5 | — | 1.14 |
| LACM 117441 | Anthill Collection (LACM 1871) | 2.1 | — | — | 1.11 |
| LACM 117373 | Anthill Collection (LACM 1871) | — | 2.1 | — | 1.17 |
| LACM 9339 | Wolff Ranch (LACM 20051) | 1.9 | — | 1.27 | — |
| SDSM 59158 | Monroe Creek Fm. (SDSM V59) | — | 2.1 | — | 0.83 |
| UCMP 105066 | *Meniscomys hippodus* (UCMP V-6506-1) | — | 0.7 | — | 0.37 |
| UCMP 105058 | *Meniscomys hippodus* (UCMP V-6506-2) | — | 0.6 | — | 0.33 |

[1]Measured from level of apex of posterior dentinal tract to lowermost margin of labial enamel.

DE1 = Depth of labial enamel on $M_1$.
DE2 = Depth of labial enamel on $M_2$.
W1 = Transverse width of enamel on $M_1$.
W2 = Transverse width of enamel on $M_2$.

respect to the bases of the lakes. This suggests that the dentinal tracts may not be as vertically extensive as in UWBM 38075.

## Lower Third Molar

This tooth is missing in the little worn dentition of the Deep River Formation, UWBM 38103, but is just emerging from the alveolus in SDSM 6277 and is present in ISU 18594. Several third molars are recognizable among the isolated teeth of the anthill collection. The mesostylid crest in the $M_3$ of SDSM 6277 and specimens of the anthill collection is, unlike the development in $M_{1-2}$, absent or incomplete. Metalophulid II extends from the ectolophid near the protoconid to the metaconid. An anterolingual fossettid is therefore not formed in these specimens. In ISU 18594 the mesostylid crest is complete. In *Meniscomys hippodus* the mesostylid crest is complete, as in $M_{1-2}$.

The region of the posterior fossettid in the $M_3$ of SDSM 6277, the anthill collection and ISU 18594 is shallower and anteroposteriorly shorter than that of $M_{1-2}$. This correlates with the size of the talonid, which is restricted in anteroposterior length. The posterolophid and ectolophid join at the hypoconid in an acute, labially prominent *V*, in correlation with a posterolabial flattening of the hypoconid. In *Meniscomys hippodus* the hypoconid is not flattened on its posterior surface, which is strongly convex, and the axis of the posterior fossettid is anteroposteriorly aligned. The hypolophid is frequently weak or absent in the specimens from South Dakota, but is present and moderately strong in *Promylagaulus lemhiensis*.

The labial inflection of $M_3$ in ISU 18595, SDSM 6277 and the anthill collection is more expansive anteroposteriorly than in $M_{1-2}$. No posterolabial fossettid is enclosed between hypoconid and mesoconid. A distinct labial spur is present on the mesoconid of ISU 18594 but is reduced or absent in the samples from South Dakota. The labial inflection of $M_3$ in *Meniscomys hippodus* is little if any larger than that of $M_{1-2}$, and a posterolabial fossettid is present.

The $M_3$ of ISU 18594, SDSM 6277 and the anthill collection is distinctly smaller in occlusal dimensions than $M_{1-2}$. In *Meniscomys hippodus* the size of $M_3$ more closely approximates that of the anterior molars.

## Upper Incisor

The upper dentition of the Deep River taxon is unknown but in the Lemhi Valley collection all upper teeth are represented. The anthill collection contains teeth representing $P^4$, $M^1$, $M^2$, $M^3$, but not $P^3$ (L. Macdonald 1972:25–26). The dentition in the type of *Promylagaulus riggsi* (FMNH P26256) consists of the upper incisor, $P^3$, and well worn $P^4$–$M^3$.

The upper incisor in the Lemhi Valley collection is gently convex across the anterior face, the medial and lateral margins of which turn posteriad at approximately equal angles. The tooth closely resembles that of *Promylagaulus riggsi*, except that it is larger. The upper incisor in *Meniscomys* is similarly proportioned but appears to be anteroposteriorly relatively shorter in cross section.

## Upper Third Premolar

The $P^3$ of *Promylagaulus riggsi* and the Lemhi collection is more slender and strongly compressed than that of *Meniscomys*. The crown lacks a basal swelling which is characteristic of *Meniscomys*. The long axis of the occlusal outline trends anterolabiad (Fig. 6a), whereas that in *Meniscomys* is aligned anteriorly or anterolingually. There is no distinct anterior or posterior carina on the crown, whereas both structures are present in *Meniscomys*. The tooth is curved from root to apex of crown, with the concave side facing anterolinguad, whereas the axis in *Meniscomys* is straight. The axial curvature in *P. riggsi* and UM 5285 places the apex of the tooth well forward of $P^4$, so that occlusal contact with $P_4$ during mastication may have been impossible. The worn surface in *P. riggsi* is polished and rounded, suggesting that only food abrasion, not contact wear, has occurred. In the Lemhi specimens no wear is apparent. A distinct facet, indicating contact wear, is characteristic of the $P^3$ in *Meniscomys*.

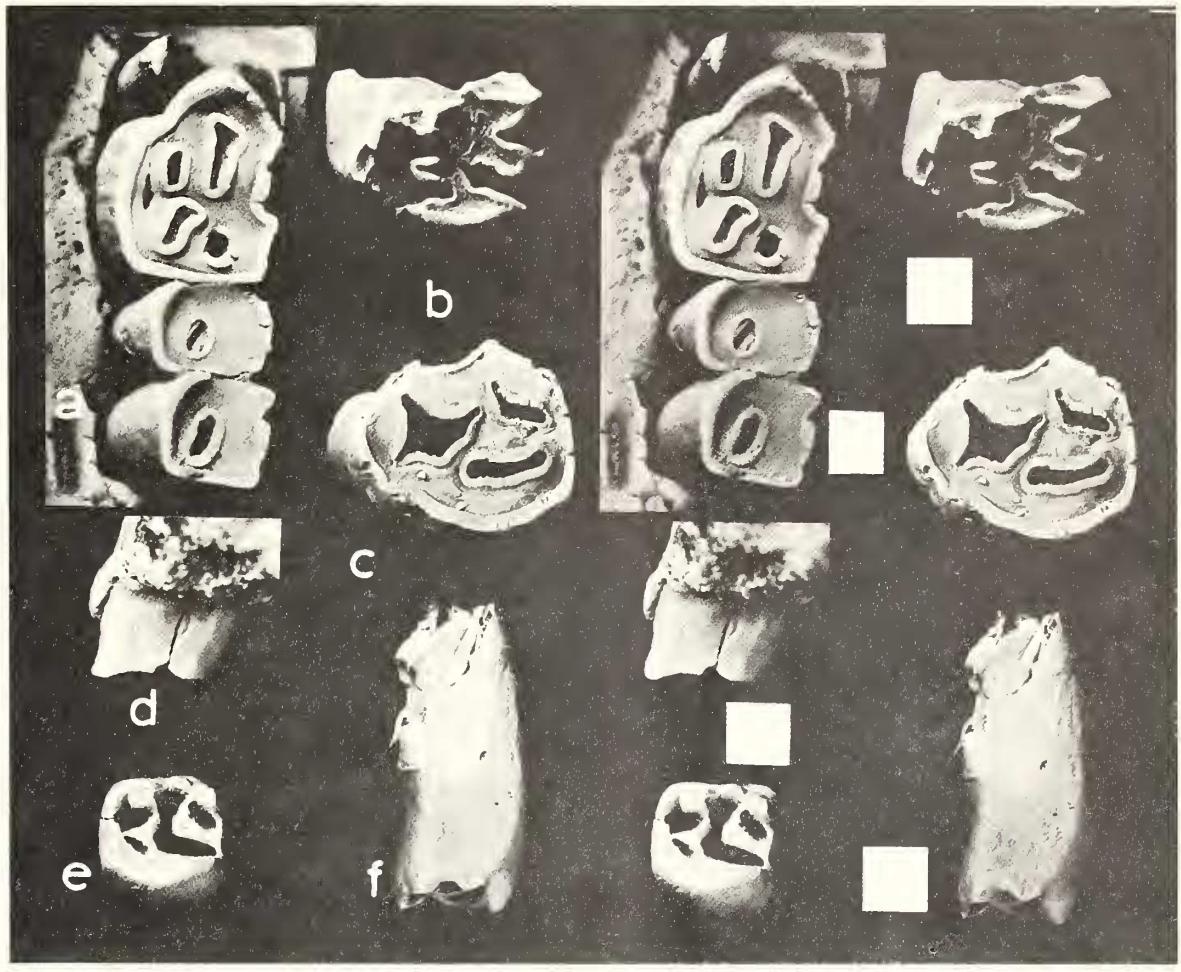


FIGURE 6. *Promylagaulus*, stereo views of upper cheek teeth. *a–P. riggsi*, occlusal view left $P^3$–$M^2$, FMNH P26256; *b–P. ovatus*, occlusal view little worn left $P^4$, LACM 117434, locality LACM 1871; *c–P. ovatus*, occlusal view worn left $P^4$, LACM 117378, locality LACM 1871; *d–P. riggsi*, posterior view left $M^2$, FMNH P26256; *e–P. ovatus*, occlusal view left $M^1$ or $M^2$, LACM 117428, locality LACM 1871; *f*–same, posterior view. Scale = 1 mm.

## Upper Fourth Premolar

The $P^4$ of the Lemhi collection is larger than that of the anthill collection. This tooth is smallest in *Promylagaulus riggsi* (Table 5). The anterocone, the anterolabial cusp characteristic of the $P^4$ of aplodontoids (Fig. 6a–c), is more lingually expanded in the specimens from the anthill locality and Lemhi Valley than in *Meniscomys*, and extends into the area occupied in the latter by a distinct cusp, the anterostyle. The anterostyle is poorly developed and sometimes absent in specimens of the anthill collection. The parastyle and mesostyle (Fig. 6a–c) are thinner and less prominent labially than in *Meniscomys*, and virtually absent in some individuals. A distinctive feature, shared by *Promylagaulus riggsi* and the specimens of the anthill and Lemhi collections, is a slight lingual displacement of the labial enamel just anterior to the mesostyle. The planes of vertical enamel in front of and posterior to the mesostyle more nearly approximate one another in *Meniscomys*. The worn occlusal outline of the tooth in the anthill and Lemhi collections (Fig. 6c) lacks much of the anterolingual notch between the region of the anterocone and the region of the protocone in *Promylagaulus riggsi* (Fig. 6a), making the tooth appear more oval. In the worn $P^4$ of *P. riggsi* (Fig. 6a), the plane of wear in the region of the parastyle and anterocone is more steeply inclined posteriad than in the teeth of the Lemhi Valley and anthill collections (Fig. 6c). No appression facet for $P^3$ is present on $P^4$ in the specimens of the anthill collection, which suggests that, as in *P. riggsi* and the Lemhi collection, the crown of $P^3$ does not occlude with $P_4$ during normal mastication. An appression facet is normally present in *Meniscomys hippodus*.

A conspicuous difference in the occlusal pattern from that in *Meniscomys* is the presence in all specimens of *Promylagaulus* of extreme anteroposterior length in the protocone, and corresponding lingual flatness of the cusp (Fig. 6b). The outline of the worn tooth in *Promylagaulus* is normally elongate anteroposteriorly

TABLE 5

Length and Width of Upper Cheek Teeth (mm)

| MUSEUM NUMBER | LOCALITY, TAXON | LP4/ | WP4/ | LM1/ | WM1/ | LM2/ | WM2/ |
|---|---|---|---|---|---|---|---|
| UM 4038 | *P. lemhiensis* (UMV 7303) | 4.0 | 3.3 | 2.1(H) | 2.9 | 2.4 | 2.7 |
| UM 5193 | Lemhi Valley (UMV 7303) | — | — | 2.2(H) | 2.9 | 2.2 | 2.7 |
| UM 5285 | Lemhi Valley (UMV 7303) | 4.4 | 3.7 | 2.5(H) | 3.0 | 2.7 | 2.8 |
| ISU 18601 | Lemhi Valley (ISU 18601) | — | 3.9 | 2.9(H) | 3.3 | 2.4 | 2.8 |
| LACM 117376 | Anthill (LACM 1871) | 3.5 | 2.6 | — | — | — | — |
| LACM 117377 | Anthill (LACM 1871) | 3.5 | 2.4 | — | — | — | — |
| LACM 117378 | Anthill (LACM 1871) | 3.5 | 2.8 | — | — | — | — |
| LACM 117380 | Anthill (LACM 1871) | 3.5 | 2.8 | — | — | — | — |
| LACM 117418 | Anthill (LACM 1871) | — | — | 1.9 | 2.0 | — | — |
| LACM 117422 | Anthill (LACM 1871) | — | — | 2.0 | 1.9 | — | — |
| LACM 117425 | Anthill (LACM 1871) | — | — | 1.8 | 1.7 | — | — |
| LACM 117374 | Anthill (LACM 1871) | — | — | — | — | 2.0 | 2.0 |
| LACM 117419 | Anthill (LACM 1871) | — | — | — | — | 2.0 | 1.9 |
| LACM 117424 | Anthill (LACM 1871) | — | — | — | — | 1.9 | 1.8 |
| LACM 117417 | Anthill (LACM 1871) | — | — | — | — | 2.1 | 2.0 |
| FMNH P26256 | *P. riggsi* | 3.3 | 2.6 | 1.5 | 2.0 | 1.7 | 2.0 |

LP4/ = Anteroposterior length of $P^4$, at occlusal surface.
WP4/ = Transverse width of $P^4$ at level of labial flexure of crown (below basal swelling).
LM1/ = Anteroposterior length of $M^1$ at occlusal surface (wear: H = heavy).
WM1/ = Transverse width of $M^1$ at occlusal surface.
LM2/ = Length of $M^2$ at level of labial flexure of crown.
WM2/ = Transverse width of $M^2$ at level of labial flexure of crown (below basal swelling).

(Fig. 6a–c), whereas the anteroposterior and transverse dimensions are almost equal in *Meniscomys*. The paracone, protoconule, and metaconule are also quite elongate anteroposteriorly and exhibit flattened labial and lingual surfaces. This trend toward lophodonty is advanced over that known for *Meniscomys*, although a similarly directed trend has commenced in the latter (Rensberger, in manuscript).

The crown of the premolar in the anthill and Lemhi collections and *Promylagaulus riggsi* is curved along the vertical axis, which is lingually convex and labially concave (Fig. 6b). Both labial and lingual surfaces are vertically convex in *Meniscomys*, so that the axis appears rather straight. The anterolingual fossette is altogether absent in one unworn specimen of the anthill collection, frequently disappears in early wear (Fig. 6c), and is absent in known specimens of the Lemhi collection (Nichols 1976). This fossette is present in both *P. riggsi* and *Meniscomys*. The area normally occupied by the anterolingual fossette in most aplodontoids is partially reached in the specimens of *Promylagaulus* lacking it by the anteriorly elongate posterolingual fossette and the lingually expanded anterolabial fossette. The posterolingual fossette is aligned almost anteroposteriorly in the Lemhi and anthill collections (Fig. 6c), whereas it slants anterolabially in *P. riggsi* (Fig. 6a) and *Meniscomys*.

## Upper Molars

The upper molars, like the premolar, are largest in the Lemhi collection and smallest in *Promylagaulus riggsi* (Fig. 7). The molars of *P. riggsi*, especially $M^{1-2}$, are rather rectangular in occlusal outline, and the anteroposterior length is less than the width (Fig. 6a). In the anthill and Lemhi collections the length and width are subequal (Fig. 6e). Poor development or lack of the mesostyle, at least in late wear, and limited lingual convexity contribute to the rectangular shape. In the little worn molars of the anthill collection, the anteroposterior length may be greater than the width, but with wear the width increases to essentially the length. In the stage of wear in which the labial (vertical) flexure of the crown has reached the occlusal surface, the length in the anthill collection is approximately equal to the width, whereas the width exceeds the length at the same stage in the Lemhi collection and *P. riggsi* (Table 5). In all groups including *Meniscomys*, the anteroposterior length of $M^1$ shortens more rapidly with wear than does that of $M^2$. The molars in *Meniscomys* bear strong mesostyles and strongly convex lingual mar-

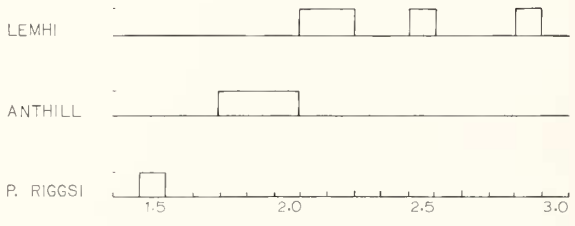


FIGURE 7. Frequency distributions of anteroposterior length of $M^1$ in specimens of *Promylagaulus* at localities Lemhi Valley (UM V-7303 = ISU 59003) and Anthill (LACM 1871), with value for type of *P. riggsi*. Base measurements for classes are listed.

TABLE 6

Depth[1] of Lingual Enamel on $M^1$, $M^2$ (mm)

| MUSEUM NUMBER | LOCALITY, TAXON | DE1/ | DE2/ | DE1/ WM1/ | DE2/ WM2/ |
|---|---|---|---|---|---|
| LACM 117417 | Anthill (LACM 1871) | — | 2.9 | — | 1.38 |
| LACM 117419 | Anthill (LACM 1871) | — | 2.3 | — | 1.15 |
| LACM 117424 | Anthill (LACM 1871) | 2.2 | — | 1.16 | — |
| LACM 117428 | Anthill (LACM 1871) | — | 2.3 | — | 1.21 |
| ISU 18601 | Lemhi (ISU 59003) | 2.0+ | 1.9+ | 0.61+ | 0.56+ |
| UM 5285 | Lemhi (UMV 7303) | — | 2.2 | — | 0.82 |
| UM 4038 | *P. lemhiensis* (UMV 7303) | — | 2.4+ | — | 0.89+ |
| FMNH P26256 | *P. riggsi* | — | 1.4 | — | 0.70 |
| UWBM 29232 | *Meniscomys hippodus* (UWA 5183–2) | — | 0.5 | — | 0.23 |

[1]measured from level of apex of posterior enamel-dentine chevron to uppermost margin of lingual enamel.

WM1/ = Transverse width of $M^1$ near apex of posterior dentinal tract.
DE1/ = Depth of lingual enamel on $M^1$.
WM2/ = Transverse width of $M^2$ near apex of posterior dentinal tract.
DE2/ = Depth of lingual enamel on $M^2$.

gins. The width of $M^1$ or $M^2$ in *Meniscomys* is greater than the length in all but the earliest stages of wear. The transverse dimension of the anterior margin of the tooth in the three groups of *Promylagaulus* is only slightly if at all less than that of the posterior margin (Fig. 6e), whereas a very narrow anterior dimension is characteristic of *Meniscomys*. With moderate wear, only the posterolingual fossette remains in *Promylagaulus*, whereas several of the smaller fossettes are present until late stages of wear in *Meniscomys*.

The unworn $M^3$ in the anthill collection contains anterolabial, anterolingual, posterolabial and posterolingual fossettes, but no central fossette. The posterolabial fossette is usually the largest and deepest, although in several specimens the posterolingual fossette is dominant. A single, probably posterolabial, fossette is present in the well worn $M^3$ of *Promylagaulus riggsi* and the Lemhi collection. In *Meniscomys* the central fossette is present and moderately persistent, and the posterolabial fossette is the largest and deepest.

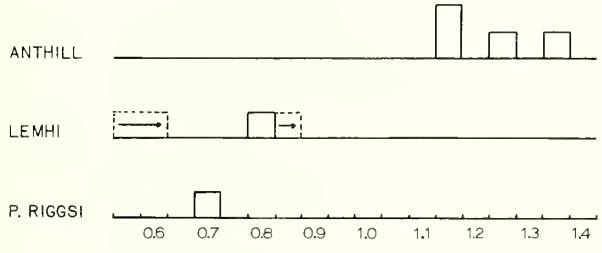


FIGURE 8. Frequency distributions of ratio of depth of lingual enamel above lowermost point of posterior dentinal tract to width of $M^1$ or $M^2$ in *Promylagaulus*. Localities as listed for Fig. 7. Base measurements for classes are listed. Arrows indicate incomplete measurements.

As in $P^4$, the crowns of the molars in *Promylagaulus* are vertically curved with the concave side labial (Fig. 6f). No comparable curvature is apparent in *Meniscomys*. Long dentinal tracts extend down the anterior and posterior sides of the molars in the anthill collection. A tract is visible on the posterior side of the left $M^2$ in *P. riggsi* (Fig. 6d) but is shallower than the corresponding plate in specimens of the anthill collection (Fig. 6f). The margins of the chevron-shaped enamel edges bordering the dentinal tracts are more steeply inclined in the anthill specimens (Fig. 6f) than in *P. riggsi* (Fig. 6e) and suggest greater hypsodonty. Furthermore, the lingual enamel plate, measured from the apex of the chevron (lowest part of the tract), is considerably longer in the anthill specimens than in *P. riggsi* (Fig. 8 and Table 6). This difference in enamel length is, for example, approximately equivalent to the change in length of the enamel of the upper and lower molars spanning three chronologically successive taxa of early Miocene pocket gophers, *Entoptychus minor*, *E. cavifrons*, and *E. transitorius* (Rensberger 1971:79–85). The depth of the lingual enamel relative to tooth width on $M^2$ is apparently intermediate in the Lemhi collection between that of *P. riggsi* and that in the anthill collection (Fig. 8 and Table 6). The roots of the upper molars in the anthill collection are greatly reduced compared to those in the Lemhi collection and *P. riggsi*.

## SYSTEMATIC PALEONTOLOGY

### Order RODENTIA

### Superfamily Aplodontoidea Matthew 1910

### Family Mylagaulidae Cope 1881

### *Promylagaulus* McGrew 1941

GENOTYPIC SPECIES: *Promylagaulus riggsi* McGrew 1941.

DEFINITION (REVISED): More hypsodont than *Meniscomys*. $P^3$ slender, curving anterolinguad, with long axis of cross section slanting anterolabiad, lacking occlusal contact. $P^4$ with lingually

expanded anterocone, parastyle and mesostyle more reduced than in *Mylagaulodon*, ectoloph anterior to mesostyle displaced linguad, protocone expanded anteroposteriorly and relatively flat lingually, posterolabial fossette smaller, less persistent than in other mylagaulids or *Meniscomys*, anterolingual fossette reduced or absent, posterolingual fossette extended craniad, anterolabial fossette expanded linguad.

$M^{1-2}$ rectangular in occlusal outline, at least in earlier stages of wear; with mesostyle reduced or absent, tendency for anteroposterior elongation of lower part of crown, persistence of posterolingual fossette long after others have worn away. $P^4-M^2$ with vertically elongate, curved (labially concave) crowns, anterior and posterior dentinal tracts.

$P_4$ with long, strong metastylid crest from metaconid to mesostylid, enclosing lingual fossettid; mesostylid usually indistinct; mesoconid flattened labially in mature stages of wear; poor development of anterior branch of labial inflection, smaller than in other mylagaulids or *Meniscomys*, extensive development of posterior branch; posterolabially compressed, anteriorly expanded hypoconid, narrow entrance to labial inflection.

$M_1$ with strong central fossettid. $M_{1-2}$ with strong metastylid crest; hypoconid posterolabially compressed, anteriorly expanded; posterolophid posteriorly convex; posterior fossettid trending anterolabiad; metalophulid II extending to apex of metaconid; crest from mesostylid bending craniad to join center of metalophulid II; anterior and lingual fossettids present; mesostylid indistinct, lacking lingual prominence, especially on $M_1$; tendency to lose rectangular outline and labial inflection in late wear.

$M_3$ with hypoconid posteriorly flattened; labial inflection relatively larger anteroposteriorly than in $M_{1-2}$; absolute occlusal dimensions much smaller than those of $M_{1-2}$; no mesostylid crest; metalophulid II extending from metaconid to protoconid; no posterolabial fossettid.

SPECIES: *P. riggsi* McGrew, L. Mioc. S. Dak.; *P. ovatus* (n. sp.) L. Mioc., S. Dak.; *P. lemhiensis* Nichols, L. Mioc. Idaho; *P. montanensis* (n. sp.) L. Mioc. Montana.

## *Promylagaulus riggsi* McGrew 1941

(Fig. 6a,d)

McGrew, P.O., 1941, Figs. 1, 2c, 3.

TYPE: Skull, lacking anterior extremities of nasals, zygomatic arches and cranium posterior to orbits; with right and left I, $P^3-M^2$; right $M^3$; FMNH P26256.

TYPE LOCALITY: Four miles south of Porcupine, South Dakota.

STRATIGRAPHIC POSITION: "Top of lower Rosebud beds" (McGrew 1941:6); "Probably Rosebud Formation" (J.R. Macdonald 1963:179). Monroe Creek Formation or Harrison Formation or Rosebud Formation (L. Macdonald 1972:25).

AGE: Arikareean or Hemingfordian, early or middle Miocene, based on the range of possible stratigraphic positions cited above. Older than late Arikareean, based on comparative stages of advancement of other species.

REFERRED SPECIMEN: SDSM 59158, $M_2$, from locality SDSM V59.

DIAGNOSIS (REVISED): Smaller than other species. Worn occlusal surface of anterocone on $P^4$ with pronounced inclination posteriad; anterolingual fossette of $P^4$ present in known specimen; posterolingual and anterolabial fossettes more restricted than in *P. ovatus, P. lemhiensis;* posterolingual fossette with strong anterolabial slant; worn occlusal outline with distinct notch separating anteriorly prominent anterocone from protocone; with angular posterolingual corner.

Anteroposterior length of $M^1$ and $M^2$ becoming less than transverse width well before wear reaches labial flexure of crown; ratio of depth of lingual enamel on $M^2$ to width of tooth 0.70, less than in other species; sides of posterior dentinal tract of $M^{1-2}$ less vertical than in other species.

## *Promylagaulus lemhiensis* Nichols 1976

Nichols, R., 1976, Figs. 7, 8b; Pl. 1, Figs. 5–10.

TYPE: Fragment of rostrum and palate with root of right I, worn left $P^3-M^2$, UM 4038.

TYPE LOCALITY: Big Wash (Univ. of Montana locality MV 7303, in part). NW¼NW¼ sec. 17, T. 17 N., R. 25 E., Lemhi quadrangle, Idaho.

STRATIGRAPHIC POSITION: Specimens from middle part of 400 foot section, Peterson Creek beds, an informal unit (Nichols, 1976).

ZONE: Upper *Meniscomys* Concurrent-range Zone (Nichols, 1976:13).

AGE: Arikareean, early Miocene.

REFERRED SPECIMENS: UM 5193, cranial and mandibular fragments with worn $M^{1-3}_{2-3}$; UM 4039, worn $P^4$; UM 4055, little worn $P^4$; UM 5285, partial skull with I, worn $P^3-M^3$; ISU 18594, mandible with little worn $P_4$, moderate to little worn $M_{1-3}$; ISU 1860I, associated $P^4$ (fragment), $M^{1-3}$, $P_4$. All from a series of closely related exposures, University of Montana locality MV 7303 (= ISU 59003); ISU 18594 from stratigraphically 21 m above type specimen.

DIAGNOSIS (REVISED): Overall size greater than that of *P. riggsi, P. ovatus.* Occlusal surface of anterocone on $P^4$ nearly horizontal in mature stages of wear; anterolingual notch, posterolingual corner of tooth less pronounced than in *P. riggsi,* making occlusal shape more oval; posterolingual fossette aligned more nearly anteroposteriorly than in *P. riggsi;* tooth in known specimens lacking distinct protoconule and anterolingual inflection.

Transverse width of $M^{1-2}$ greater than anteroposterior length at level of labial flexure of crown, as in *P. riggsi,* unlike *P. ovatus;* ratio of depth of lingual enamel of $M^2$ above apex of posterior dentinal tract to width of tooth 0.82–0.89+, greater than in *P. riggsi,* less than in *P. ovatus.* Root branches of $M^{1-2}$ more prominent than in *P. ovatus.*

Posterior and lingual fossettids of $P_4$ wider relative to tooth width (ratios 0.41, 0.30, resp.) than in *P. montanensis;* central width of tooth greater relative to overall width than in *P. montanensis* (ratio 0.67); length (4.7–5.0 mm) greater than in *P. montanensis, P. ovatus;* ratio of depth of labial enamel to length of tooth (.43–.44) less than in *P. ovatus, P. montanensis.*

Ratio of depth of labial enamel on $M_2$ to tooth width (0.95) less than in *P. ovatus.* Metastylid crest of $M_{1-2}$ with less posterior prominence than in *P. montanensis;* no posterolingual fossettid, unlike *P. montanensis;* labial inflection relatively more expansive anteroposteriorly than in *P. montanensis;* central posterior convexity less pronounced than in *P. montanensis.* Heavier layer of cementum overlapping enamel of cheek teeth than in *P. ovatus, P. montanensis.*

## *Promylagaulus ovatus*[1] NEW SPECIES
(Figs. 3a–f; 6b,c,e,f)

Macdonald, J.R., 1970, Fig. 14 *(Promylagaulus* cf. *riggsi).*
Macdonald, L., 1972:25–26 *(Promylagaulus riggsi).*

TYPE: Little worn left $M_2$. LACM 117435.

TYPE LOCALITY: Anthills of LACM 1871 (=SDSM V6229) SW ¼, sec. 9, T. 39N., R. 42 W., east of Porcupine Creek, Sharps Corner quadrangle, South Dakota.

STRATIGRAPHIC POSITION: Upper part of Monroe Creek Formation (Harksen 1970). Fossils, although recovered from anthills, apparently derived from two or three 0.6 cm thick bone bearing layers in nearby vertical cliffs (Harksen, 1970; L. Macdonald 1972:6). Locality may be at transition between Monroe Creek and Harrison formations (James E. Martin, pers. comm.).

ZONE: *Entoptychus-Gregorymys* Concurrent-range Zone (Fisher and Rensberger 1972).

AGE: Arikareean, early Miocene.

REFERRED SPECIMENS: LACM 117351–117370, 117372, 117392, 23530, 23532, 23535, 23536 ($P_4$); 117373–117375, 117403, 117406, 117410–117416, 117438–117441, 23534 (lower molars); 117384, 117436, 23637 ($DP_4$); 117376–117383, 117385–117391, 117393–117396, 117434, 23538 ($P^4$); 117371, 117397–117400, 117404, 117405, 117407, 117417–117433, 23528, 23529, 23531, 23534 (upper molars); from locality LACM 1871.

SDSM 6277, right mandible, $DP_4$–$M_3$; from locality V6210.

LACM 9339, right $M_1$; LACM 9340, right $P_4$; LACM 9342, right $P_4$; from locality LACM 2005, northeast of Wolff Ranch, South Dakota.

DIAGNOSIS: Smaller than *P. montanensis* and *P. lemhiensis,* slightly larger than *P. riggsi.* Worn occlusal surface of anterocone on $P^4$ less inclined posteriad than in *P. riggsi;* anterolingual fossette of $P^4$ only occasionally absent in unworn premolars, but frequently disappearing with early wear; posterolingual fossette expanded anteriad, with more nearly anteroposterior alignment than in *P. riggsi;* anterolingual notch and posterolingual corner less pronounced than in *P. riggsi,* making occlusal shape oval.

Transverse width of $M^1$ or $M^2$ approximately equal to anteroposterior length at level of vertical flexure of labial surface; ratio of depth of lingual enamel to width of tooth 1.15–1.21, greater than in *P. riggsi, P. lemhiensis;* sides of dentinal tracts more nearly vertical than in *P. riggsi;* root branches of less prominence than in *P. lemhiensis.*

Posterior and lingual fossettids of $P_4$ wider relative to tooth width (ratios 0.32–0.36, 0.27) than in *P. montanensis,* possibly narrower than in *P. lemhiensis;* ratio of depth of labial enamel to length of tooth 0.49–0.54, less than in *P. montanensis,* greater than in *P. lemhiensis.*

Ratio of depth of labial enamel on $M_1$ or $M_2$ to tooth width 1.11–1.27, greater than in *P. lemhiensis, P. riggsi;* metastylid crest with less posterior prominence than in *P. montanensis;* no posterolingual fossettid, unlike *P. montanensis;* labial inflection relatively more expansive anteroposteriorly, shallower transversely than in *P. montanensis;* labial part of posterolophid less extensive anteriorly than in *P. montanensis;* deep portion of posterolophid more protuberant posterolabially (less posteriorly) than in *P. montanensis.*

DISCUSSION: An isolated cheek tooth from the anthill locality was selected as the type of this species in lieu of the mandible from SDSM V6210, because of the much larger sample of *Promylagaulus* as well as other mammalian taxa at the anthill site. Furthermore, the cheek teeth are poorly exposed in the young mandible, leaving doubt as to the stage of advancement in hypsodonty.

It seems likely from this evidence that *P. riggsi,* for which the stratigraphic occurrence is uncertain, did not occur in a deposit which was contemporaneous with those of the anthill locality and other sites which have yielded *P. ovatus.* The preservation of the specimens also suggests this conclusion. The specimens of *Promylagaulus* from the anthill locality, that from SDSM V6210, and those from the Wolff Ranch locality (LACM 2005), all of which are referable to *P. ovatus,* are of medium to dark or blackish brown color, whereas the teeth of *P. riggsi* are very light in color.

Placement of the occurrences of *Promylagaulus ovatus* in the *Entoptychus-Gregorymys* Concurrent-range Zone is based upon the abundant association of *Gregorymys formosus* (L. Macdonald 1972:30) and the advanced morphology of *Promylagaulus* compared with that of *Meniscomys. Meniscomys* occurs only stratigraphically beneath the *Entoptychus-Gregorymys* Concurrent-range Zone in the John Day Formation (Fisher and Rensberger 1972).

## *Promylagaulus montanensis* NEW SPECIES
(Fig. 2)

TYPE: Right mandible with $DP_4$, $M_{1-2}$, incisor fragment; missing upper part of ascending ramus. UWBM 38103.

TYPE LOCALITY: Spring Creek 1 (UWA 5867–1). SE-NW trending draw 46°37.4′ N, 111°3.6′ W; SE¼ sec. 14, R. 5 E., T. 10 N., Hanson Reservoir quadrangle, Montana.

STRATIGRAPHIC POSITION: Deep River Formation. Specimens from stratigraphically lower of two units. Brownish tan, massive sandstone.

ZONE: *Entoptychus-Gregorymys* Concurrent-range Zone.

AGE: Arikareean, early Miocene.

REFERRED SPECIMEN: Right mandible with worn $P_4$–$M_3$; lacking incisor, ventral margin, condylar process and ascending ramus; geographic locality and stratigraphic position exactly that of type specimen. UWBM 38075.

DIAGNOSIS: Larger than *P. ovatus* and *P. riggsi.* Anteroposterior length of $P_4$ 4.1 mm, less than in *P. lemhiensis;* ratios of width of posterior and lingual fossettids to tooth width less than in *P. lemhiensis, P. ovatus;* ratio of depth of labial enamel to length of tooth 0.68, greater than in *P. ovatus, P. lemhiensis;* ratio of central width to overall width of tooth 0.55, smaller than in *P. ovatus, P. lemhiensis.*

Metastylid crest of $M_{1-2}$ with greater posterior prominence than in *P. ovatus, P. lemhiensis;* small posterolingual fossettid on $M_2$, incipient posterolingual fossettid on $M_1$, unlike *P. ovatus, P. lemhiensis;* labial inflection anteroposteriorly more compressed, transversely relatively deeper than in *P. ovatus, P. lemhiensis;* central posterior convexity of posterolophid more pronounced than in *P. ovatus, P. lemhiensis.*

DISCUSSION: The placement of this form in the *Entoptychus-Gregorymys* Concurrent-range Zone is based upon an associated assemblage of taxa, including *Gregorymys,* to be described later.

---

[1]*ovatus:* L., egg shaped, in reference to the occlusal outline of $P^4$.

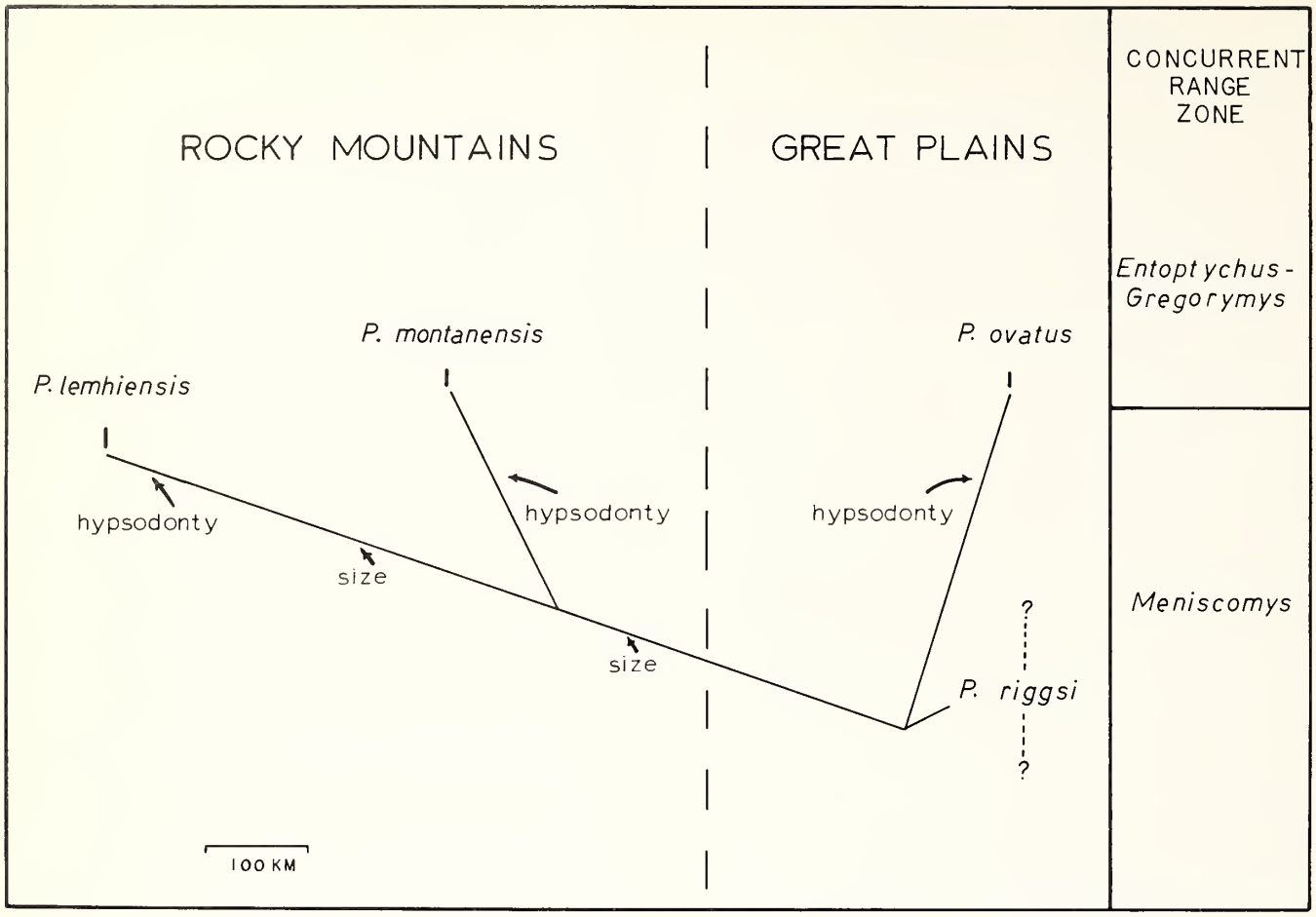


FIGURE 9. A possible phylogeny for the described species of *Promylagaulus* which would explain the morphological and geographical differences. Arrows designate chronologic intervals during which increases in size and hypsodonty presumably occurred. The stratigraphic position of *P. riggsi* is uncertain.

## *Promylagaulus* sp.

McKenna and Love 1972, Figs. 15, 16.

LOCALITY: Darton's Bluff (AMNH) Big Horn Mountains, SW¼NE¼, sec. 19, T. 48 N., R. 85 W., Hazelton Peak quadrangle, Johnson County, Wyoming. Exposure along bluff near head of Canyon Creek.

STRATIGRAPHIC POSITION: In 22 m thick, light tan, grading upward to light gray, massive, fine-grained sandstone within 43 m Miocene section.

ZONE: *Entoptychus-Gregorymys* Concurrent-range Zone.

AGE: Later Arikareean, early Miocene.

MATERIAL: Right mandible, $P_4$–$M_2$, I; left mandible $P_4$–$M_3$, fragmentary incisor. Posterior parts of both rami missing. AMNH 56333.

DISCUSSION: Judging from the illustrations of this specimen, it may be distinct from *Promylagaulus ovatus, P. montanensis, P. riggsi,* and *P. lemhiensis*. Lingual enamel is present on the occlusal surface at a stage of wear in which the occlusal outline is oval, unlike the condition in *P. ovatus*. In late stages of wear in *P. ovatus,* the originally rectangular outline remains until the lingual enamel disappears. The Wyoming specimen more closely resembles *P. montanensis* and *P. lemhiensis* in this character. However, the size is smaller than that of *P. montanensis, P. lemhiensis,* or *P. riggsi* and the dentinal tracts seem to be less extensive than in *P. montanensis,* judging from the greater continuity of enamel surrounding the heavily worn molars. It appears to be more hypsodont than *P. riggsi*.

That this occurrence seems to be within the *Entoptychus-Gregorymys* Concurrent-range Zone is based upon the presence of *Entoptychus* as well as the association with what may be *Pleurolicus* (McKenna and Love 1972:17–21). Although these geomyoids are not contemporaneous in the John Day Formation, the range of *Entoptychus* commences immediately above the range of *Pleurolicus* (Fisher and Rensberger 1972:24).

## PHYLETIC RELATIONSHIPS OF THE SPECIES

The greater size of the species of *Promylagaulus* from the Rocky Mountains and the fact that the most primitive form, *P. riggsi,* is the smallest suggests that the group may have originated in the Great Plains. *P. ovatus,* the youngest known form in the Plains, was only slightly larger than *P. riggsi* but conspicuously advanced in hypsodonty. The species occurring farthest west, *P. lemhiensis,* is the largest but is only slightly more hyp-

sodont than *P. riggsi*. These relationships suggest (Fig. 9) that an early divergence from the primitive stock may have dispersed westward and radiated again in the Rocky Mountain region. The amount of time involved in this dispersal, diversification and evolution was apparently not very great, judging from the occurrences of both *P. montanensis* and *P. ovatus* in the *Entoptychus-Gregorymys* Concurrent-range Zone, probably low in that zone, and *P. lemhiensis* in deposits not much older.

## RELATIONSHIPS OF *PROMYLAGAULUS*

McGrew (1941:26), followed by subsequent workers, placed *Promylagaulus* in the Mylagaulidae. He believed, although with a degree of uncertainty regarding several characters, that *Promylagaulus* gave rise to *Mylagaulodon* and therefore to later mylagaulids. As McGrew noted, the upper premolar of *P. riggsi* displays the same general features as FMNH P26266 and is intermediate in degree of hypsodonty between the latter and *Meniscomys hippodus*. Wilson (1960:54) noted an apparent difference in the number of lakes in the molar talonid of *Promylagaulus* and *Mesogaulus*, but was uncertain as to whether wear in the specimen of *Promylagaulus* accounted for the discrepancy. Other characters in the worn dentition of *P. riggsi* raise at least some doubt about a relationship to the mylagaulids. The better represented taxa, *P. ovatus* and *P. lemhiensis*, unknown at the time of those earlier studies, exhibit features which differ more clearly from those of the mylagaulids.

The mesostyle in $P^4$, an early character in aplodontids and which in *P. riggsi* can be interpreted as almost worn away, is much smaller in *Promylagaulus* than in *Mylagaulodon* (FMNH P26266). The posterolabial fossette of $P^4$ is small and is worn away well before the other two major fossettes disappear in *P. ovatus*, whereas in the mylagaulids this structure is as persistent as the other fossettes, and in *Mylagaulodon* is large. The labial inflection of $P_4$ is undivided in *P. ovatus* and *P. lemhiensis* but is divided in both *Meniscomys* and the mylagaulids (for the latter see Black and Wood 1956, Fig. 1). The posterolabial fossettid of the lower molars, the one queried by Wilson, is absent or vestigial in the molars of *Promylagaulus*, relatively larger in *Meniscomys*, and still larger in *Mesogaulus* (Wilson 1960, Fig. 59) and *Mylagaulus* (McGrew 1941, Fig. 12). However, the posterolabial inflection above the fossettid is formed differently in *Mesogaulus* than in either *Meniscomys* or *Promylagaulus*, for in occlusal view (Black and Wood 1956, Figs. 8B,E) the channel is elongate, extends strongly posterolinguad, and the anterolabial margin of the hypoconid doesn't hook toward the mesoconid but joins the base of the protoconid to close the fossettid. In both *Meniscomys* and *Promylagaulus* the posterolabial fossettid is small and oval, and is formed by union of the anterolabial process of the hypoconid with the mesoconid.

One of the distinctive characters of *Promylagaulus* is the posterolabial flattening of the hypoconid in $P_4$–$M_3$. The hypoconid is usually rather protuberant posterolabially in *Mesogaulus* (Wilson 1960, Figs. 56–59; Black and Wood 1956, Figs. 6, 8), but in the unworn pattern of the molars may extend anterolabiad somewhat as in *Promylagaulus*.

On the other hand, *Promylagaulus* shares with the later mylagaulids reduction of the labial prominence of the stylar cusps in the upper cheek teeth and the tendency for the occlusal outlines to become oval. It also shares relatively large $P^4_4$ and, unlike the aplodontines, persistent fossettids. Although the reduction of stylar structures may have occurred independently, these events may have emerged from an early common adaptive trend and affinity.

The morphology of the mylagaulids and *Promylagaulus* seems therefore to suggest that the mylagaulids may possibly have evolved from a lineage leading eventually to *Promylagaulus*, as opposed to others going toward other aplodontoids, but if so, the ancestral form for *Promylagaulus* and the mylagaulids was so primitive that the posterolabial inflection of the lower molars was still unclosed — a stage more primitive than that of any aplodontid presently known from the *Meniscomys* Concurrent-range Zone.

*Promylagaulus* may represent a progressive group that was part of a rather profuse radiation of aplodontoid rodents in the early Miocene just prior to and during the *Meniscomys* Concurrent-range Zone, of which only a few groups, not *Promylagaulus*, survived into the middle Miocene.

## ACKNOWLEDGMENTS

I wish to thank the following people for providing access to specimens used in this study: Drs. Lawrence G. Barnes, Theodore Downs, and David P. Whistler, LACM; Drs. Philip E. Bjork and Morton Green, SDSM; Dr. William D. Turnbull, FMNH; Dr. Robert W. Fields and Mr. Ralph Nichols, UM; and Dr. John A. White, ISU. I am grateful to Drs. Craig C. Black and Mary R. Dawson of the Carnegie Museum, Dr. Donald L. Rasmussen of the Amoco Production Company, and Dr. David P. Whistler of the LACM, who read the manuscript and offered suggestions which greatly improved it. Mr. and Mrs. Ben Witte and Mr. David Nunnallee were of much assistance in the field work that produced the specimens from the Deep River Formation. This study was supported in part by N.S.F. Grant GB 35959.

## LITERATURE CITED

Black, C.C. and A.E. Wood. 1956. Variation and tooth replacement in a Miocene mylagaulid rodent. Jour. Paleontology 30:672–684.

Fisher, R.V. and J.M. Rensberger. 1972. Physical stratigraphy of the John Day Formation, central Oregon. Univ. Calif. Publ. Geol. Sci., 101:45 p.

Harksen, J.C. 1970. Geology of the Sharps Corner quadrangle. In: Macdonald, J.R., 1970. Review of the Miocene Wounded Knee faunas of southwestern South Dakota. Los Angeles County Mus. Nat. Hist. Bull. 8:82 p., 2 maps.

Macdonald, J.R. 1963. The Miocene faunas from the Wounded Knee area of western South Dakota. Amer. Mus. Nat. Hist. Bull. 125:141–238.

_____ . 1970. Review of the Miocene Wounded Knee faunas of southwestern South Dakota. Los Angeles County Mus. Nat. Hist. Bull. 8:82 p., 2 maps.

Macdonald, L. 1972. Monroe Creek (early Miocene) microfossils from the Wounded Knee area, South Dakota. South Dakota Geol. Surv. Rept. Investig. 105:43 p.

McGrew, P.O. 1941. The Aplodontoidea. Field Mus. Nat. Hist. Geol. Ser. 9:1–30.

McKenna, M.C. and J.D. Love. 1972. High-level strata containing early Miocene mammals on the Big Horn Mountains, Wyoming. Amer. Mus. Novitates 2490:31 p.

Nichols, R. 1976. Early Miocene mammals from the Lemhi Valley of Idaho. Tebiwa 18:9–47.

RENSBERGER, J.M. 1971. Entoptychine pocket gophers (Mammalia, Geomyoidea) of the early Miocene John Day Formation, Oregon. Univ. Calif. Publ. Geol. Sci. 90:209 p.

_____. 1975. *Haplomys* and its bearing on the origin of the aplodontoid rodents. Jour. Mammalogy 56:1–14.

_____. (manuscript). Aplodontoid rodents of the John Day Formation.

STIRTON, R.A. 1935. A review of the Tertiary beavers. Univ. Calif. Publ. Bull. Dept. Geol. Sci. 23:391–457.

WILSON, R.W. 1960. Early Miocene rodents and insectivores from northeastern Colorado. Univ. Kansas Paleontological Contr. Vertebrata 7:92 p.

Accepted for publication June 1, 1978.